FLORAL ATTRACTION AND FLORAL HAIRS IN THE COMMELINACEAE¹

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ABSTRACT

Commelinaceae flowers are visited mainly by a great variety of bees and syrphid flies. A buzz mechanism associated with poricidal anthers is the most specialized pollination system reported. From a distance, inflorescences and associated structures may attract pollinators visually. At close range, the corolla is almost always showy, and sometimes the calyx is also conspicuous. The androecium is attractive because it produces pollen, the only reward supplied by the flower. Yellow, nearly pollenless anthers, antherodes, hairs, and broad connectives may deceptively attract insects. Floral odors may also attract pollinators. They are taxonomically widespread but uncommon in the family. None have been investigated chemically and a role in pollination has not been demonstrated. Floral hairs related to pollination are largely confined to the androecium and occur widely in the family. Their function may include attracting insects to the flowers (either toward or away from the main source of pollen), providing footholds, retaining fallen pollen, and determining how insects behave on the flower, including how they collect pollen.

The Commelinaceae are a family of herbaceous monocots consisting of 40 genera and approximately 640 species (Faden & Hunt, 1991). The two outstanding features of Commelinaceae flowers that affect their reproductive biology are the lack of nectar and brief flowering times (generally a few hours, always less than a day). The lack of nectar has two important consequences: (1) the flowers rarely attract whole classes of pollinators, notably butterflies, moths, birds, and bats; and (2) the pollen must serve two functions, pollination and rewarding the pollinator. The short anthesis limits certain reproductive strategies, such as the temporal separation or sequential development of the male and female sexual organs or functions in the flower.

The purpose of this paper is to present and discuss two aspects of floral biology within the Commelinaceae: how plants attract pollinators, both visually and with floral scents, and the possible reproductive functions of floral hairs. The literature on floral biology in the family is limited, so much of what will be presented is anecdotal or inferential. It is hoped that bringing together what is known will stimulate further research on pollination and floral biology in Commelinaceae.

POLLINATION OF COMMELINACEAE

Commelinaceae flowers are chiefly entomophilous or autogamous. The main insect visitors are social and solitary bees and syrphid flies. Additional insects that I have recorded on Commelinaceae flowers include other Diptera, various families of Coleoptera, Hemiptera, Homoptera, Orthoptera, Thysanoptera, and occasional ants (Hymenoptera: Formicidae) (Faden, unpublished). Rare butterfly visits have been recorded (Knuth, 1909: 476; Schuster & Schuster, 1971), although I have never observed any. In addition to bees and syrphid flies, potential pollinators include bee flies (Bombyliidae) and some beetles (Melyridae, Buprestidae, Mordellidae, and possibly other families).

The flowers of Commelinaceae species that have been studied in some detail are recorded as being visited by a variety of insects. At the low end is Tinantia anomala (Torrey) C. B. Clarke, from which only four bee species plus unidentified syrphid flies were noted (Simpson et al., 1986). At the other extreme are Tripogandra serrulata (Vahl) Handlos, on which no fewer than 14 species of bees, six of syrphid flies, and six of other insect

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orders were recorded (Schuster & Schuster, 1971), and Commelina erecta L., from the flowers of which 42 species of insects were collected, including nine species of bees and four of syrphid fly (Faden, unpublished). Even some mainly autogamous species may be visited by numerous insects, e.g., annual species of Tripogandra (Handlos, 1970). My field research on Commelina erecta in Texas (Faden, unpublished) and on numerous African Aneilema species (Faden, 1991 and unpublished) suggested that for many Commelinaceae, the longer that a species is observed, the greater the diversity of insects that will be found visiting its flowers.

The only specialized pollination system to have been documented in the family is a buzz mechanism, which has been reported in two unnamed species of Dichorisandra (Sigrist & Sazima, 1991). Such a mechanism had been predicted for Cochliostema (Vogel, 1978), and it is also likely to be found in species of the several genera, e.g., Porandra, that have apical poricidal anther dehiscence. The unusual floral odor in Palisota hirsuta (Thunb.) Schumann suggests an unusual pollinator (see below), but there are insufficient field observations.

The behavior of insects on the flowers has been described for several Commelinaceae, e.g., Tinantia anomala (Simpson et al., 1986) and Tripogandra serrulata (Schuster & Schuster, 1971), but behavioral descriptions generally have not indicated the probable effectiveness of the insect as a pollinator. Callisia repens L. is the only—or certainly one of the very few—Commelinaceae that is probably anemophilous.

Commelinaceae for which there are recent data about flower visitors and pollination are: Aneilema species (Faden, 1983, 1991, and unpublished), Commelina erecta L. (McCollum et al., 1984; Faden, unpublished), Commelina tuberosa L. (as C. communis) (Brantjes, 1980), Dichorisandra species (Sigrist & Sazima, 1991), Tinantia anomala (Torrey) C. B. Clarke (Castro, 1978 (as Commelinantia anomala); Simpson et al., 1986), Tradescantia species (Sinclair, 1967, 1968), Tripogandra serrulata (Vahl) Handlos (as T. cumanensis) (Schuster & Schuster, 1971), and Tripogandra species (Handlos, 1970).

VISUAL ATTRACTION OF POLLINATORS

Commelinaceae attract pollinators mainly visually. Their flowers are usually brightly colored. Commonly, however, the flowers are quite small, and, in such cases, it may be the inflorescences and/or associated structures that attract pollina-

tors, especially from a distance. The most extreme example of this occurs in Coleotrype madagascarica C. B. Clarke of Madagascar, in which the upper leaves on the flowering shoot are bright pink basally, with similarly colored sheaths, matching the color of the corollas of the flowers that are borne in sessile, sheath-perforating inflorescences at the bases of these leaves. In Spatholirion longifolium (Gagnepain) Dunn the inflorescence axis and cincinni are bright purple and would seem to be much more conspicuous from afar than the tiny flowers. Even in Cochliostema, which has among the largest flowers in the Commelinaceae, the long, pink bracts (on the peduncle and at the bases of the cincinni) and pink peduncle and axes may enhance the conspicuousness of the flowers.

Inflorescences may be more striking than the individual flowers when the calyces are colored and accrescent, as in species of Amischotolype (e.g., A. philippensis (Merrill) ined.) and some populations of Tinantia leiocalyx C. B. Clarke. In Floscopa, the faded flowers, which typically have colored, long-haired sepals, persist even when they fail to set fruit. In that genus, as well as others with small-flowered species, e.g., Aneilema, Callisia, Palisota and Tripogandra, the dense inflorescences with numerous flowers create a visual impact that the same-sized flowers more loosely arrayed would fail to impart.

At close range the individual flowers and their parts are conspicuous. With the exception of a few species of Callisia, e.g., C. repens, the petals are always obvious, even when small, ranging from white through various shades of pink, blue or violet or, rarely, yellow to orange. In zygomorphic flowers one petal may be reduced and inconspicuous, as in species of Aneilema and Commelina. All three petals have strikingly fringed margins in Cochliostema, Geogenanthus, and a related, undescribed, neotropical genus.

The sepals are most commonly green and inconspicuous, but sometimes they are tinged or suffused with red or purple, e.g., species of Aneilema and Tradescantia; colorfully streaked or striped, e.g., Aneilema hockii De Wild.; entirely brightly colored and contrasting with the corolla, e.g., species of Amischotolype; or similar in size and color to the petals (petaloid), e.g., Palisota and Streptolirion. Colored, accrescent and persistent sepals have been mentioned above. In any of these cases the sepals would be expected to play a role in attracting pollinators.

The androecium attracts insects because it produces pollen, the only reward supplied by the flower. The common differentiation of the androecium into two morphologically distinct sets of stamens, or stamens and staminodes, reflects the duality of function: attracting insects yet limiting the amount of pollen they collect. The parts of the androecium that specifically may attract potential pollen vectors are anthers, connectives, filament hairs, pollen, and anther- or pollenlike structures (staminodes, hairs, and connectives).

As the source of pollen, the anthers should be the focus of an insect's attention. This should be true whether the pollen is exposed, as in most genera; is enclosed within apically poricidal anthers (species of Cartonema, Amischotolype, Coleotrype, Dichorisandra, and Porandra); or is more elaborately sequestered, as in Cochliostema. Structures that resemble pollen or create the impression of more pollen than is actually present may also attract (or distract) insects, particularly when the true anthers are less conspicuously colored, e.g., concolorous with the petals (Vogel, 1978; Brantjes, 1980). Thus, yellow antherodes or nearly pollenless anthers, e.g., Aneilema, Murdannia and Commelina, yellow-bearded stamen filaments, e.g., Tinantia, Geogenanthus, and Cochliostema, and broad, yellow anther connectives, e.g., Tradescantia, may deceptively attract pollinators (Vogel, 1978).

Filament hairs (discussed below) and connectives may also be attractive to insects, aside from mimicking pollen. In Callisia fragrans (Lindley) Woodson, the corolla is inconspicuous, but the anther connectives are broad and white and resemble six tiny flags in each flower, probably providing the visual attraction generally furnished by the corolla in other Commelinaceae. In some Aneilema species, e.g., A. rendlei C. B. Clarke, bees visiting the flowers generally first alight on the greatly expanded, colorful connective of the middle stamen (Faden, 1991, and unpublished). Similarly, in many species of Commelina, e.g., C. hockii De Wild. and C. forskaolii Vahl, the medial stamen anther is more striking than the laterals because of contrasting markings on its broad connective (Faden, unpublished).

Ultra violet (UV) light absorption and reflectance have been little investigated in the Commelinaceae. Handlos (1970: 62) reported the flowers of Cochliostema odoratissimum Lemaire and Tradescantia pallida (Rose) D. H. Hunt (as Setcreasea pallida) to reflect UV light. Simpson et al. (1986) showed that the upper anthers and surrounding hairs in Tinantia anomala absorb UV light, in contrast with the UV-reflecting petals behind them.

FLORAL ODORS

Floral odors as attractants of pollinators have not been discussed previously for the Commelinaceae as a whole. They are taxonomically widespread but uncommon in the family. Strong odors have been reported in Callisia fragrans (as Spironema fragrans) (Lindley, 1840), Cochliostema odoratissimum (Lemaire, 1859), Tradescantia subacaulis Bush and T. roseolens Small (Anderson & Woodson, 1935), and Tripogandra grandiflora (Donnell-Smith) Woodson (Handlos, 1970). The strongest odors that I have noted were in Callisia fragrans (cultivated plant of unknown provenance), Callisia multiflora (Martens & Galeotti) Standley (cultivated plant originally from Mexico), Cochliostema odoratissimum (cultivated plant originally from Ecuador), Palisota alopecurus Pellegrin (population in Cameroon), P. bracteosa C. B. Clarke (cultivated plants of unknown provenance), and P. hirsuta (cultivated plants originally from Ghana and Nigeria, and one plant in Cameroon). The reported fragrance by Read (1965) in Cochliostema velutinum Read was not characterized as strong or weak, but it is likely to have been relatively strong because the original collector had noted it.

Weak floral scents are more common than strong ones, but they too seem to be infrequent in the family. Handlos (1970) reported very faint scents in Tripogandra amplexicaulis (C. B. Clarke) Woodson, T. purpurascens (Schauer) Handlos, and T. saxicola (Greenman) Woodson, all from Mexico. I have recorded weak odors in populations of the eastern North American Tradescantia ernestiana Anderson & Woodson (in Arkansas), T. gigantea Rose (Louisiana), T. hirsuticaulis Small (Arkansas), T. hirsutiflora Bush (Arkansas), and T. ozarkana Anderson & Woodson (Arkansas); eight (all African) out of approximately 33 species of Aneilema (the others were odorless) (Faden, 1991); Tinantia erecta (Jacq.) Schldl. in Mexico (also cultivated plants from Bolivia); and greenhouse-cultivated plants of Commelina stefaniniana Chiov. (from Somalia), Dichorisandra thyrsiflora Mikan (from a plant originally cultivated in Peru), Palisota barteri Hook. (from Ghana), and Stanfieldiella brachycarpa (Mildbr.) Brenan (from Gabon). Peace Corps volunteer Bruce Kahn (in litt.) recently reported a slight scent in the flowers of a Cameroonian population of Pollia condensata C. B. Clarke, the only record of a floral odor in this genus.

Interspecific variation in floral odor production

or strength has been noted in several species. In Aneilema johnstonii Schumann some populations were recorded as having weakly fragrant flowers and other populations as odorless (Faden, 1991). Among research plants of Tinantia erecta from many populations cultivated in 1988 at the Botanic Garden of the University of Copenhagen I noted some with slight fragrances and others with no odor. Some individual plants in a population of Tradescantia hirsutiflora had scented flowers and other plants unscented ones (Faden, unpublished). I consider Palisota hirsuta flowers to be strongly scented, but Peace Corps volunteer Bill Keating records (in sched.) only a "slight smell" in a Cameroonian population. This reported difference is, I suspect, a matter of judgment or definition of "strong" and "weak" odors. However, it could also be due to genetic variation among populations, differences in the observer's perception (olfactory sensitivity), the number and density of open flowers in the area, the temperature (higher temperature causing greater volatility and stronger scent), and the conditions under which the flowers are smelled (e.g., in the field vs. a closed greenhouse).

No floral scent in the Commelinaceae has been investigated chemically. Nearly all odors have been characterized merely as "pleasant" or "fragrant," but flowers of Tradescantia subacaulis have been described more precisely as violet-scented, and those of T. roseolens as having the fragrance of tea-roses (Anderson & Woodson, 1935). I have recorded the weaker odor of T. hirsuticaulis as violet-scented and those of T. ernestiana, T. gigantea, and T. ozarkana as rose-scented. The odor in Pollia condensata, mentioned above, was recorded as lemon-scented. The only convincingly recorded nonfragrant scented flowers occur in Palisota hirsuta. They are mushroom-scented.

The source of the odor within the flower has been little investigated. When several flowers of Aneilema somaliense C. B. Clarke were dissected into sepals, petals, staminodes, stamens, and gynoecium, the staminodes seemed to be at least one source of the scent, but the results were inconclusive (Faden, 1991: 26). In Palisota hirsuta the copious but sterile pollen of the upper two stamens is the chief or sole source of the mushroom scent (Faden, unpublished). In Cochliostema odoratissimum the fragrance is produced by the petals (Faden, unpublished).

FLORAL HAIRS

Hairs may occur on all floral parts. Their functions probably include defense against insect feed-

ing, protection from desiccation, and pollination. Only their role in pollination will be discussed here. Pollination-related hairs may be present on all floral whorls, but they occur mainly on the androecium. The only sepaline hairs showy enough possibly to be involved in pollination are found in Floscopa. The fringing, petaline hairs in Cochliostema, Geogenanthus, and a related, undescribed genus may contribute to the attractiveness of these flowers. Gynoecial hairs are usually confined to the ovary and are probably protective, but some species of Cyanotis have bearded styles, with colorful, moniliform hairs similar to those of the stamen filaments in the same flowers. Very likely they have the same functions as the staminal hairs (discussed below).

Although absent in many genera, such as Commelina, androecial hairs are common in the Commelinaceae (Table 1), and their function is probably related to pollination in nearly all cases. They may function in several ways, including attracting insects to the flower and either to or away from the main source of pollen. They may affect how and where insects move within the flower and how they collect pollen. Finally, the presence or absence of staminal hairs may determine, in part, the kinds of insects that visit a flower.

Hairs may be present and similar on all filaments, as in most actinomorphic flowers, e.g., Tradescantia and Cyanotis. In many zygomorphic flowers, however, they occur only on specific filaments, e.g., the two lateral stamens in Aneilema or the three upper stamens in Geogenanthus. In Tinantia flowers the filament hairs vary in length, color, abundance, and position on the filament among the five bearded filaments (the sixth is glabrous). In genera having the antesepalous androecial whorl differentiated from the antepetalous whorl, e.g., Murdannia, Palisota, and Tripogandra, the differences commonly include filament pubescence (Table 1).

Filament hairs differ in structure and conspicuousness. They are most commonly moniliform, i.e., composed of beadlike cells, but in Aneilema they are never moniliform (Faden, 1991), and in Tripogandra the hairs may be moniliform or not, depending on the species (Handlos, 1970, 1975). Some unusual filament hair types, e.g., glandular hairs, hook-hairs, and branched hairs, are apparently confined to Aneilema and are described by Faden (1991). The hairs may be minute (< 0.5 mm) and inconspicuous (e.g., all species of Aneilema sect. Brevibarbata), but usually they are long and evident.

TABLE 1. Filament hairs in the Commelinaceae (generic circumscription and arrangement follow Faden & Hunt, 1991).

All filaments bearded		All filaments glabrous		Some filaments bearded, some glabrous	
Triceratella Triceratella		Cartonema			
Tradescantieae		Tradescantieae		Tradescantieae	
Streptolirion Spatholirion Aethiolirion³ Cyanotis Belosynapsis Coleotrype Porandra Amischotolype Cochliostema®	Thyrsanthemum Gibasoides Matudanthus Elasis Gibasis Tradescantia Callisia Tripogandra Sauvallea	Coleotrype ¹ Dichorisandra Siderasis Geogenanthus ⁵ Weldenia Tradescantia ⁶ Callisia		Palisota Aethiolirion² Geogenanthus¹ Tinantia Tripogandra	
Commelineae		Commelineae		Commelineae	
Murdannia		Stanfieldiella Floscopa Buforrestia Murdannia Anthericopsis Tricarpelema Pseudoparis	Polyspatha Dictyospermum Pollia Aneilema Rhopalephora Commelina	Murdannia Aneilema Tricarpelema	

¹ Coleotrype lutea H. Perrier only.

When staminal hairs contribute to the general showiness of the flower, some role in attracting pollinators may be inferred. This is particularly likely where the filaments are densely bearded with long, colored hairs that extend well beyond the corolla, e.g., Aneilema sect. Pedunculosa, Cyanotis and Tradescantia, and where the hairs contrast in color with the petals, e.g., some species of Cyanotis and Aneilema. In species of Cyanotis, Tradescantia, and Tripogandra the pink to blue or violet (sometimes partly white) hairs often closely surround the yellow anthers, seemingly drawing attention to them. In Streptolirion volubile Edgew. and Aneilema chrysopogon Brenan the hairs below the anthers are yellow, which may draw attention to the anthers either because of the color contrast with the corollas, or because there may appear to be more pollen present than the flowers actually provide.

Vogel (1978) cited Tinantia and Cochliostema as genera in which yellow hairs mimic pollen and deceptively draw pollinators to them. To this list can be added Geogenanthus. In Tinantia the upper three stamens have small anthers surrounded by yellow hairs. Vogel terms them "advertising stamens." The lower stamens, with longer filaments, have larger, more polliniferous anthers that are more cryptically colored. Bees should focus on the upper anthers and brush against the lower ones and the style. The pattern in Geogenanthus rhizanthus (Ule) Brueckner, as determined from herbarium specimens, appears to be similar to Tinantia, except that the upper filaments are more densely bearded and there is less of a size difference between the upper and lower anthers.

The only yellow color in Cochliostema flowers is a tuft of hairs on the upper surface of the central, columnlike structure that is composed of the upper

² Staminate flowers only.

³ Perfect flowers only.

⁴ Rarely all filaments bearded.

⁵ Geogenanthus ciliatus Brueckner only.

⁶ Few species only.

⁷ Occasionally both sets of stamens bearded.

⁸ A small glabrous staminode sometimes present.

⁹ Tricarpelema glanduliferum (Joseph & R. Rao) Faden only.

three stamens whose greatly expanded connectives completely enclose their anthers. Vogel (1978) suggested that insects trying to collect pollen from the yellow hairs probably cause pollen to be shed from the anthers by vibration.

Simpson et al. (1986) have made the only detailed study in Commelinaceae that tests Vogel's deception hypothesis. Working with *Tinantia anomala* in Texas, they found that the upper stamens are more obvious to insects than to humans and the lower stamens less so, owing to differences in UV absorption/reflectance in different parts of the flower. They discovered that the upper stamens produced about half as much pollen as the lower, that pollen grains from the upper anthers were about 8% shorter than the lower anther pollen, and that pollen from both sets of anthers was equally fertile.

The main visitors to the flowers were syrphid flies and bees. Syrphid flies focused on the upper anthers but did not contact the stigma. Large native bees, such as Bombus pennsylvanicus, landed on the upper stamens and contacted the stigma with their abdomen, but their visits were infrequent. Smaller bees were more common, and Agapostemon texanus visited both sets of stamens, but the authors do not consider these bees significant pollinators. The most abundant visitor was the introduced honeybee, Apis mellifera, which, unlike the native bees, first foraged on the lower anthers, then the upper, while regularly contacting the stigma.

Simpson et al. (1986) concluded that Tinantia anomala does not support Vogel's hypothesis because few native insects of the proper size to effect pollination behave in the predicted manner, and because the upper anther pollen is fertile and the plant autogamous. However, Simpson et al. do confirm that native insects focus on the upper stamens, as predicted, and that at least the larger native bees are effective pollinators. Because T. anomala is autogamous, it requires out-crossing only to maintain genetic diversity, not for seed production. Therefore, although there seems to be a great waste of pollen in this species, it is still possible that native bees provide the necessary level of out-crossing.

There is little direct evidence that filament hairs affect how insects "work" flowers. In species of Aneilema sect. Brevibarbata the stamen filament hairs are inconspicuous because they are minute (sometimes < 0.5 mm long), usually colorless, and are attached on the lower surface of the sigmoid lateral stamen filaments (Faden, 1991). In flowers of A. umbrosum (Vahl) Kunth subsp. umbrosum in Ghana I observed small bees (probably Lasio-

glossum sp., Halictidae) hanging upside down from the bearded portion of the stamen filament, head facing the base of the flower, while the rear legs collected pollen from the anther (Faden, unpublished). Thus, these tiny hairs may serve as footholds for insects.

Staminal hairs may serve to retain pollen that falls or is dislodged from the anthers, maintaining it in a position where it is both accessible to insects for collection and can also contact them ventrally (Renner, pers. comm.). In *Cyanotis* the staminal hairs would appear to be essential because anther dehiscence is functionally by basal pores. The pollen is squeezed out into the tangle of filament and (when present) stylar hairs and could otherwise be lost but for them.

The hairs of the densely bearded filaments in species of Tradescantia and Cyanotis may function further by interfering with pollen collection. Medium- to large-sized bees have been observed sometimes to draw together the anthers of a flower before collecting pollen (honeybees on Aneilema johnstonii in Zambia; Amegilla sp. (Anthophoridae) on Aneilema hockii in Kenya; Faden, unpublished), which might increase the efficiency of pollen collection (over sequential collection from individual anthers). These Commelinaceae have glabrous, divergent stamen filaments. The density of the filament hairs and their proximity to the anthers in Tradescantia and Cyanotis flowers may interfere both with the anthers being pulled together and with pollen being scraped or combed off them. The bearded style in many Cyanotis species may further keep the stamens apart. Pollen caught in the dense staminal (or stylar) hairs could not be collected rapidly. Thus, while the filament hairs in Tradescantia, Cyanotis, and probably other genera, may attract pollinators by being colorful and contrasting with the anthers, they may also reduce the efficiency of pollen collection by closely surrounding the anthers. Sinclair (1967, 1968) mentioned (and I can confirm from garden observations) that honeybees visiting Tradescantia flowers often pull all of the anthers together and then collect pollen from them. Whether native bees also do this is unknown.

The presence or absence of staminal hairs may relate to the types of pollinators that visit flowers. Because hairs provide more surface area and more footholds, they may tend to favor insects that must land in order to feed, such as smaller bees and syrphid flies. Knuth (1906: 106) recorded the filament hairs in *Tradescantia* as providing support and footholds for insects, noting that such flowers were especially favored by bees. In *Aneilema* I

have recorded more species of flies (mostly syrphid flies) than bees visiting the flowers of all three species of section Pedunculosa—characterized by long, colorful stamen filament hairs-from which flower visitors were collected. In contrast, all seven species of section Lamprodithyros—characterized by glabrous filaments—had more bee than fly species visiting their flowers. Within section Amelina, which may have either glabrous or bearded filaments, the two species sampled with glabrous filaments were visited by more bee species, and the one with long-bearded filaments by more diptera (Faden, 1991). The correlation between longbearded filaments and fly visitation in Aneilema should be considered tentative because the data for most of the Aneilema species were derived from casual collecting, not long-term studies. In any event, the diversity of insects visiting the flowers of a species is less important than the number of individuals and the effectiveness of the insect species in bringing about pollination, and these were not recorded.

DISCUSSION

The selected topics discussed in this paper, how Commelinaceae flowers attract pollinators and how floral hairs may function in pollination, may serve as an introduction to the larger subject of reproductive biology in the family. Clearly, our knowledge even of the topics discussed is quite limited. With regard to other aspects of reproductive biology, even such basic information as daily flowering times is unknown for the majority of Commelinaceae. What are most needed are more long-term field observations and experimental investigations. Studies of pollination and reproductive biology require little or no technology, and therefore they are especially well suited for students or researchers at small institutions and in developing countries. It is hoped that this paper will stimulate biologists to look more closely at the reproductive biology of locally occurring species of this nearly cosmopolitan family.

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